FIRE SEVERITY EFFECTS ON NUTRIENT DYNAMICS AND MICROBIAL ACTIVITIES IN A SIBERIAN LARCH FOREST

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A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

By

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Fairbanks, AK

August 2016

Abstract

High-latitude ecosystems store large amounts of carbon in soil organic matter and are among the most vulnerable to climate change. In particular, fire severity and frequency are increasing in boreal ecosystems, and these events are likely to have direct and indirect effects on climate feedbacks via increased emission of carbon (C) from soil and changes in vegetation composition, respectively. In this study we created experimental burns of three severities in the northeastern Siberian arctic, near Cherskiy, RU, and quantified dissolved C, nitrogen (N), and phosphorus (P), and microbial respiration and extracellular enzyme activities at 1-day, 8-days, and 1-year post-fire.

Our objective was to determine how fire affects C, N, and P pools, soil microbial processes, and how these effects scale across severity and time since fire. We found labile C and nutrients increased immediately post-fire, but appeared similar to unburned controls within a week. Phosphorus alone remained elevated through 1-year post-fire. Leucine aminopeptidase activities initially increased with fire severity, but by 1-year, activities decreased with fire severity at a rate an order of magnitude faster. Fire severity suppressed phosphatase and β-glucosidase activities at all time points. Soil respiration was reduced by half in high severity plots 1-year post-fire, while net rates of N mineralization increased by an order of magnitude. We found that changes in soil C and nutrient pools, soil respiration, and net N mineralization rates responded in a threshold-fashion to fire severity, although P was uncoupled from C and N by changing at a distinct severity threshold. Extracellular enzyme activities and edaphic variables scaled linearly with fire severity. The interaction of threshold and linear response curves to fire severity may help explain the variability across studies in soil microbial community responses to fire. Microbial communities recovering from more severe fires have the possibility to decrease

future ecosystem C losses through reduced respiration. The changing fire regime in permafrost ecosystems has the potential to alter soil microbial community dynamics, the retention of nutrients, and the stoichiometry of C, N, and P availability.

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Acknowledgments

Throughout this thesis, "we" refers to myself, Sarah Ludwig, and my coauthors, Heather Alexander, Knut Kielland, Paul Mann, Sue Natali, and Roger Ruess. This project was supported with funding from a National Geographic Research and Exploration Grant to H.D.A., National Geographic Young Explorer Grant to S.M.L., NSF grant #1044610 to S.M.N., NSF grant #1304007 to S.M.N., NSF grant #1103443 and #1304040 to H.D.A.

Introduction

As the climate continues to warm, wildfire frequency and severity are predicted to increase in high latitudes, creating a positive feedback to climate change (Flannigan et al. 2000, Kasischke et al. 2010). Fires have profound consequences for ecosystem biogeochemical cycling, both directly through the combustion of organic matter and indirectly through changing vegetation dynamics, physical environmental conditions, and resource availability (Bond-Lamberty et al. 2004, Mack et al. 2008). Consequently, soil microbial communities recovering from fire can exhibit substantial deviations in structure and function from pre-disturbed communities (Boerner et al. 2008, Bárcenas-Moreno et al. 2011, Dooley and Treseder 2011, Wang et al. 2012). Fire influences soil microbial abundance through a variety of mechanisms, including increasing or decreasing soil moisture and nutrient availability, decreasing C quantity and quality, and increasing soil temperature (Dooley and Treseder 2011). The variability in the effects fire has on microbial communities occurs across both temporal and spatial scales. As a result, there is little consensus as to the effects of fire on soil microbial communities, both within and across ecosystem types (Hart et al. 2005, Dooley and Treseder 2011, Wang et al. 2012).

High-latitude ecosystems are unique in that greater than 90% of the terrestrial C pool is stored in soil organic matter (SOM) (IPCC 2007). A substantial portion of fuel combustion from fires in high-latitudes comes from surface organic layers (Boby et al. 2010). The decomposition of soil microbes are the primary means by which soil C is released and nutrients are recycled. The recovery of soil microbes after fires in high latitudes has the potential to alter ecosystem biogeochemistry, possibly mitigating or exacerbating changes in C, N, and P (Wang et al. 2012). The uncertainty and variability in soil microbial responses to fire need to be better understood in order to accurately predict how fires will influence ecosystem functioning and feedbacks to climate change. This is especially relevant in boreal ecosystems given their vulnerability to fire and the preeminent role of soil microorganisms in ecosystem functioning.

Through combustion, fires alter soil organic matter by reducing C and N pools (Wang et al. 2012), redistributing P in ash (Wan et al. 2001), creating black carbon, and changing the fractions of dissolved and labile organic matter (Martín et al. 2009). The dissolved and labile portions of soil C and N tend to be more sensitive to disturbance. A meta-analysis by Wang et al. (2012) of 76 fire-related studies across subtropical, temperate, and boreal ecosystems found overall a slight increase in dissolved C and N after fires; however, this depended strongly on the type of fire (wild or prescribed), soil depth, and time since fire. Less than 3 months after burning, %C in dissolved organic matter increased 50-60%, but by 1 year the average declined to below 30% compared to unburned controls. Total dissolved N responded in the opposite manner with respect to time since fire. Microbial biomass C and N are particularly labile portions of the SOM pool, and were also inconsistent in both the direction and magnitude of change after fire depending on the type of fire, time, and soil depth (Wang et al. 2012). While this meta-analysis was not able to explicitly address fire severity, wildfires tend to be higher severity than prescribed burns (Walstad et al. 1990). Partial combustion of organic material creates black carbon. Black carbon is characterized by a polycyclic aromatic structure, which is resistant to both chemical and biological degradation, and carboxylic groups along the aromatic backbone, which sorb strongly to water and nutrients (Glaser et al. 2002).

In addition to altering soil resources, fires change physical conditions with large potential impacts for recovering soil microbial communities. Fire can increase pH, soil temperature, and increase or decrease soil moisture (Boerner et al. 2009, Dooley and Treseder 2011). Soil microbial activity in response to environmental changes and resource availability can play a vital role in how ecosystems recover by affecting nutrient cycling, SOM formation and turnover, and conditions for plant growth (Shenoy et al. 2013). Fire consistently reduces soil microbial respiration (Dooley and Treseder 2011), though wildfires tend to have a stronger effect than prescribed burns, likely because wildfires tend to be more severe fires (Wang et al. 2012). Net N mineralization rates can increase or decrease by as much as 50% following fire, and vary based on the time since fire and type of fire (Boerner et al. 2008).

Microbial community resource acquisition capacity can be assessed by measuring the activity of bulk soil extracellular enzymes. Extracellular enzymes are produced by microbes and exuded into the environment to cleave substrates and provide smaller more soluble forms of nutrients for microbes, and can be the rate-limiting step of decomposition (Jones and Kielland 2002, Sinsabaugh and Shah 2012). The response of extracellular activity to fire is also highly variable, with studies finding no changes, increases, or decreases (Boerner and Brinkman 2003, Boerner et al. 2008, Gartner et al. 2012, Rietl and Jackson 2012). Much of the variability in microbial activity and C, N, and P pools after fires are attributed to differences in time since fire and fire severity (Boerner et al. 2008, Wang et al. 2012).

The response of soil microbes to fire in ecosystems with permafrost is particularly important given that these ecosystems store large quantities of C and are nutrient limited. Permafrost is estimated to store approximately1600 Pg C, twice that of the C in the atmosphere (Schuur et al. 2015). High-latitude ecosystems are characterized by slow turnover of SOM due to cold, wet, and acidic conditions, and low nutrient inputs. This leads to severe nutrient limitation of primary productivity and microbial activity. The majority of boreal studies have shown primary productivity to be limited by N, P, or co-limited by the two (Hobbie et al. 2002). Wildfire is the primary disturbance in high latitude forests, and is responsible for generating patchy landscapes (Boby et al. 2010). Boreal forests are home to numerous fire-adapted plant species, and the consequences of wildfires on successional dynamics are well studied in Alaska and Canada (Johnstone and Chapin 2006, Shenoy et al. 2011). However, compared to grasslands and temperate forests, the effects of fire on soil processes are less well known in permafrost ecosystems.

In this study, we asked 1) How does fire severity affect C, N, and P pools and soil microbial activities? and 2) How do these effects change over time? To examine these questions, we created experimental burns with four severity treatments (no burn (control), low, medium, and high), and followed changes in soil C, N, and P cycling at three intervals post-fire (1-day, 8-days, and 1-year). This study was conducted in the Kolyma River watershed of Northeastern Russia, in sparse larch forest near the boreal-tundra ecotone. The Kolyma River is underlain by continuous permafrost, with a large proportion of yedoma permafrost formed during the Pleistocene and characterized by high organic matter and ice content (Zimov et al. 2006). The Russian boreal forest is relatively understudied and little is known about vegetation and soil responses to fire (Alexander 2012).

We hypothesized that immediately following fire there is a flush of resources from incomplete combustion of SOM, releasing both organic and inorganic N and P in ash and labile C that was not volatilized, and that soil microbes respond to this initial resource increase by increasing production of extracellular enzymes in concordance with growth. In contrast, microbial activities over the long term are driven by black carbon and the degree of SOM loss post-fire, collectively reducing resource availability by nutrients adsorbing to black carbon (Hart et al. 2005), increasing recalcitrance of DOM (Fernández et al. 1997, Martín et al. 2009), and suppressing microbial biomass (Dooley and Treseder 2011). Lastly, we hypothesized that as fire severity increases, so too does the initial increase in resources and microbial activity. In the long term, we expect that since more severe fires consume more of the soil organic layer, this will decrease soil respiration, microbial activity, and C, N, and P resources.

This study contributes to an important gap in our understanding of the effects of fire on ecosystem processes. Variations in fire severity has been offered as an explanation for the inconsistencies in how soil C, nutrients, and microbial communities respond to fire (Boerner et al. 2008, 2009, Wang et al. 2012). Here we explicitly test this by examining the impacts of fire from a range of severities and following these effects over time. Describing a relationship between fire severity and changes in soil C, N, and P pools will increase our ability to predict the consequences of boreal forest fires and potential feedbacks to climate through changes in soil respiration and vegetation recovery.

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Methods

Study Area

The research site was located ~0.5 km east of Northeast Science Station near Cherskiy, Sahka Republic, Russia (68.74 ^{O}N, 161.40 ^{O}E), which is approximately 250-km north of the Arctic Circle and 130-km south of the Arctic Ocean. The mean annual temperature of the area is -11.6 ^{O}C, with summer temperatures averaging 12 ^{O}C and winter temperatures -33 ^{O}C (Alexander 2012). Mean annual precipitation is 210 mm/year with approximately half falling during the summer as rain (Alexander 2012). The fire return interval is between 50-120 years (Schepaschenko et al. 2008). Vegetation at the study site can be characterized as a sparse Cajander larch (*Larix cajanderi*) forest, with understory vegetation including deciduous shrubs (*Betula divaricate, B. exilis*, *Salix spp.* and *Alnus fruticosa*), evergreen shrubs (*Vaccinium vitisidaea, Arctous alpine, A. erytrocarpa, Empetrum androgynum, Pyrola grandiflora,* and *Ledum decumbens*), herbs (*Carex appendiculata*), grasses (*Calamagrostis neglecta*), mosses (*Aulacomnium turgidum*), and lichens (*Cetraria cuculata* and *Cladina rangiferina*). Overstory trees were ~ 178 yr old and averaged 9 m tall and 16 cm in DBH. Sampling in the final study year also included two nearby early-successional larch stands (7 and 11 years since fire), which had similar vegetation composition.

Experimental Design and Burns

In July 2012, 16 experimental plots (2 x 2-m) were delineated along a gradually sloping hillside such that none were directly downhill from another. Plots were located ~ 2 m apart and at least 4 m from a mature larch tree. Each plot was randomly assigned to a burn severity treatment: control (no burn), low, medium, and high. Each plot and a 1-m wide buffer along each side was clipped of aboveground vascular vegetation prior to burning to ensure consistency among treatment effects and to prevent fire spread. Burn severity treatments were achieved by varying the fuel load allocated to each plot. Low severity treatments received 4.5 kg fine twigs (< 1 cm diameter) and leaves. The medium severity treatments received 4 kg fine twigs and leaves, 5 kg small twigs (1-2 cm diameter), and 10 kg coarse twigs (2-5 cm diameter). The high severity treatments received 11 kg fine twigs and leaves, 10 kg small twigs, 10 kg coarse twigs, and 45 kg logs (> 5 cm diameter). These fuel levels represented various woody debris loads found across mature larch forests of varying densities in the area. All fuels were collected from areas near the burned site and dried before use. Experimental burns were conducted on July 6 and 7, 2012 and were allowed to burn out naturally. Fires were started using fire starters, which are dried hay-like material covered with parafilm. No outside fuel sources (i.e., gasoline) were used in these burns.

In July 2013 two additional early-successional larch stands were sampled that burned naturally 7 and 11 years prior. Each of the burned stands were paired with an adjacent stand that had not burned in the most recent fires, 7 and 11 years ago, to serve as a control.

Soil Sampling and Analyses

Soil cores were collected from 12 of the experimental plots (three of each treatment) 1-day post fire, 8-days post fire, and 1-year post fire. For each sampling time, three cores were collected from each plot no closer than 20-cm to the edge of the plot. Two depths were sampled at each time point, the organic layer and top 10 cm of the mineral horizon. During the 1-year post-burn sampling, soils were also sampled from the bottom 10 cm of thawed mineral soil. These bottom mineral samples averaged 50 cm below the top of the thawed mineral horizon. The organic layer depth was measured at each location where a core was taken. Thaw depth was measured as the average of five places in each plot using a thaw probe. The three cores for each depth were then pooled together and homogenized. Soils were similarly sampled from the organic horizon in the two nearby early-successional stands in conjunction with the 1-year post fire sampling.

Within 24-hours of collection, soils were subsampled for soil water content, water extractions, and extracellular enzyme assays. Soil moisture was calculated as the percent change from field-wet mass after drying at 100 ^{O}C for three days. Soil organic matter content was determined from ash-free dry mass after combusting at 500 ^{O}C for 4 hours. Soil pH was measured on 5 g to 25 ml DI water slurries for organic samples and 10 g to 20 ml DI water slurries for mineral samples, in the first year of the study only. Soils were extracted with DI water in a ratio of 50 ml to 10 g soil, centrifuged at 6000 rpm for 10 min and then filtered using 0.7 μm filters. Water extractions were analyzed for dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) using a Shimadzu TOC-VCPH analyzer. Chromophoric dissolved organic matter (CDOM) was measured on water extractions using a spectrophotometer measuring absorbance from 200-800 nm. Specific UV absorbance (SUVA) and slope ratios (S_R) were then calculated following Helms (2008). Higher SUVA values indicate more aromatic CDOM, which often corresponds to more recalcitrance to decomposition. Higher S_R values correspond to lower molecular weights of CDOM, which can indicate that these compounds are more labile. Water extractions were frozen until analyzed colorimetrically for NH_4^+, NO_3^-, and PO_4^{-3}. Nitrate values were almost always below levels of detection, and henceforth we report dissolved inorganic nitrogen (DIN) as the sum of nitrate and ammonium.

The activities of extracellular enzymes involved in C, N and P acquisition were determined colorimetrically as described by Sinsabaugh et al. (1993). We assayed the activities of β-glucosidase, which breaks down cellulose providing glucose as a product, phenol oxidase, which decomposes lignin, leucine aminopeptidase, which degrades proteins and polypeptides, and acid phosphatase, which cleaves phosphate groups from organic molecules. For each assay the following substrates (respectively) were dissolved in 50 mM sodium acetate buffer (pH 5): 5 mM pNP-β-glucopyranoside, 10 mM LDOPA, 2.5 mM leucine p-nitroanilide, and 5 mM pNP-phosphate. We incubated 600 µl soil slurries with 400 µl of substrate for 4-24 hours at 17 ^{O}C and measured the formation of the colored product with a microplate reader. Extracellular enzyme activities were assayed for all organic samples and the mineral samples from 1-year post-burn.

Soil Incubations

Soils from the 1-year sampling time were incubated in the lab to measure soil respiration as well as net N mineralization rates. Two sets of 10 g subsamples were weighed fresh. The first set of subsamples were extracted with 2 M KCl within 24 hours and analyzed for DOC, TDN, NH_4^+, and NO_3^- in the same manner as the water extracts. The second set of field-moist subsamples was incubated in the dark at 17 ^{O}C. Moisture levels were maintained by weighing daily and adding DI water until the sample's mass returned to initial values. After 1 week, CO_2 flux over a one hr period was measured using an IR gas analyzer (LICOR, 6262). After incubating for 2 weeks, soils were extracted with 2 M KCl. Net inorganic N mineralization rates were calculated as the DIN after incubating, minus the initial DIN over the duration of the incubation. Net organic N production rates were calculated similarly.

Statistical Analyses

We used mixed-effects models to determine the effects of fire severity and time on soil nutrient pools and microbial activities. Treatment and time were used as fixed effects, with plot as a random effect. We only considered the grouping structure with a random intercept since both treatment and time are categorical here. We regressed residual organic layer depth, as a proxy for fire severity, against response variables when a linear model provided a better fit, again using a mixed-effects model with plot as the random effect. Model fitting was performed using the “lmer” function from the “lme4” package for R, using restricted maximum likelihood. For those variables only measured in the second year of the study we used simple ANOVA (“aov” in R) and linear regression (“lm” in R) models. We assessed the assumptions of each model using QQ-normal plots of residuals and plots of residuals against fitted values to assess heteroskedasticity. Where there was a significant effect of either treatment or time, post-hoc Tukey’s tests were run to determine pairwise differences. Where necessary data were log-transformed (used for DON, DOC, DIN, and PO_4^{3-}) to achieve equal variance. All statistical analyses were done using the statistics program “R” v2.7.0, with a significance level alpha = 0.05.

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Results

Physical and Environmental Transformations

The experimental burn treatments were effective in creating a range of fire severities (ANOVA $F_{3,8}$=8.817, p<0.01; Fig 1).

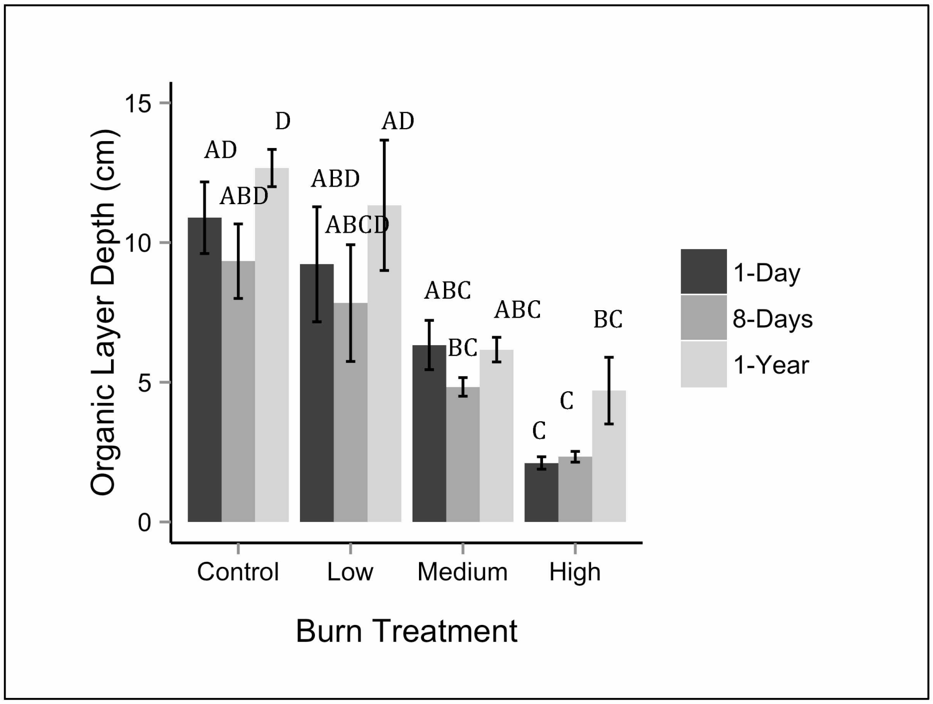


Figure 1: Organic Layer Depth
Mean residual organic layer depth along a fire severity gradient created with experimental burns on July 6, 2012 in a mature Cajander larch forest near the Northeast Science Station in Cherskiy, Russia. Average pre-fire organic layer depth was 10.3 cm +/- 0.4 cm. Error bars denote standard error; letters denote significance from a post-hoc Tukey's HSD test after fitting a mixed effects model.

The low severity treatments scorched the soil surface but barely consumed any of the organic layer. Pre-fire organic layer depths averaged 10.3 cm with a standard error of 0.4 cm. The medium severity fires consumed on average 50% of the organic layer, about 5 cm, while the high severity burns consumed 75% of the organic layer. After the first year post-fire, the high severity treatment also disturbed the soil structure by causing subsidence, and by June of the following year, thaw depths were already significantly deeper than the control plots and other treatments (ANOVA $F_{3,8}$=15.19, p<0.01; Fig 2).

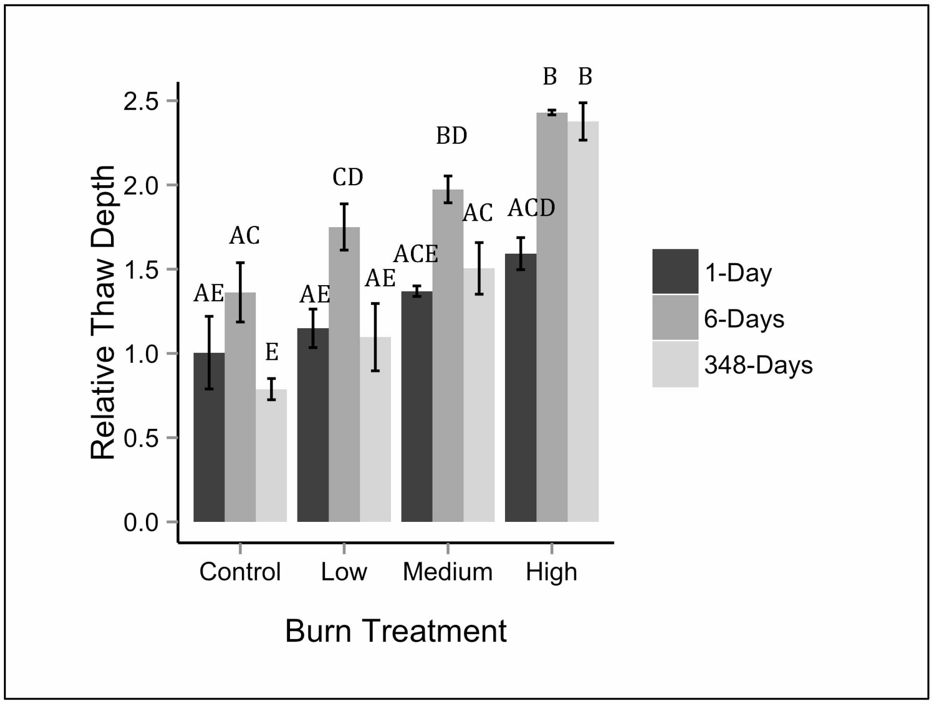


Figure 2: Relative Thaw Depth
Mean thaw depth relative to pre-burn (day 0) measurements, along a fire severity gradient created with experimental burns on July 6, 2012 in a mature Cajander larch forest near the Northeast Science Station in Cherskiy, Russia. Error bars denote standard error; letters denote significance from a post-hoc Tukey's HSD test after fitting an analysis of variance model.

In the organic horizon, soil moisture increased linearly with residual organic layer depth at all time points, and all organic horizons were drier at each successive time point (fixed effects: slope=1.5; p < 0.001, 8-days; p < 0.001, 1-year; p < 0.01; Fig 3).

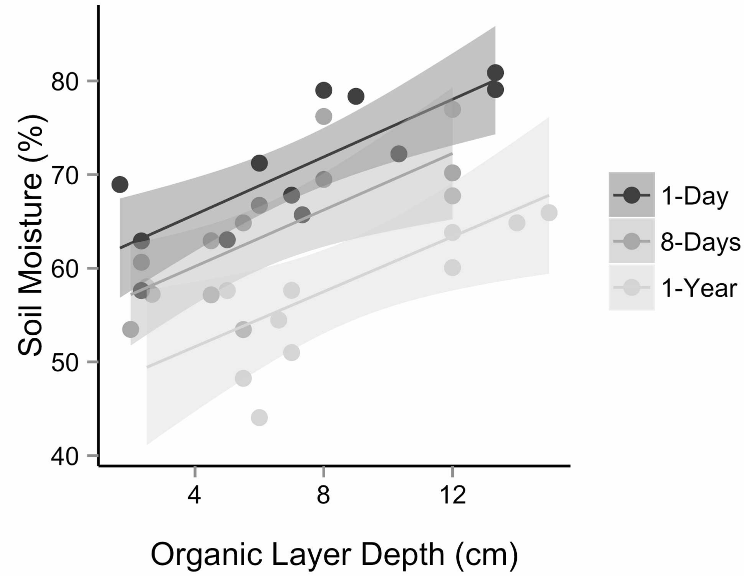


Figure 3: Soil Moisture
Organic layer % moisture (gravimetric) as a function of residual organic layer depth, along a fire severity gradient created with experimental burns on July 6, 2012 in a mature Cajander larch forest near the Northeast Science Station in Cherskiy, Russia. Regression lines and 95% confidence intervals are from a mixed effects model.

Soil pH increased with fire severity in the initial sampling, although by 8 days post-fire (fixed effects: low; $p = 0.77$, medium; $p = 0.21$, high; $p < 0.01$), none of the treatments were significantly different from the control plots (Fig 4).

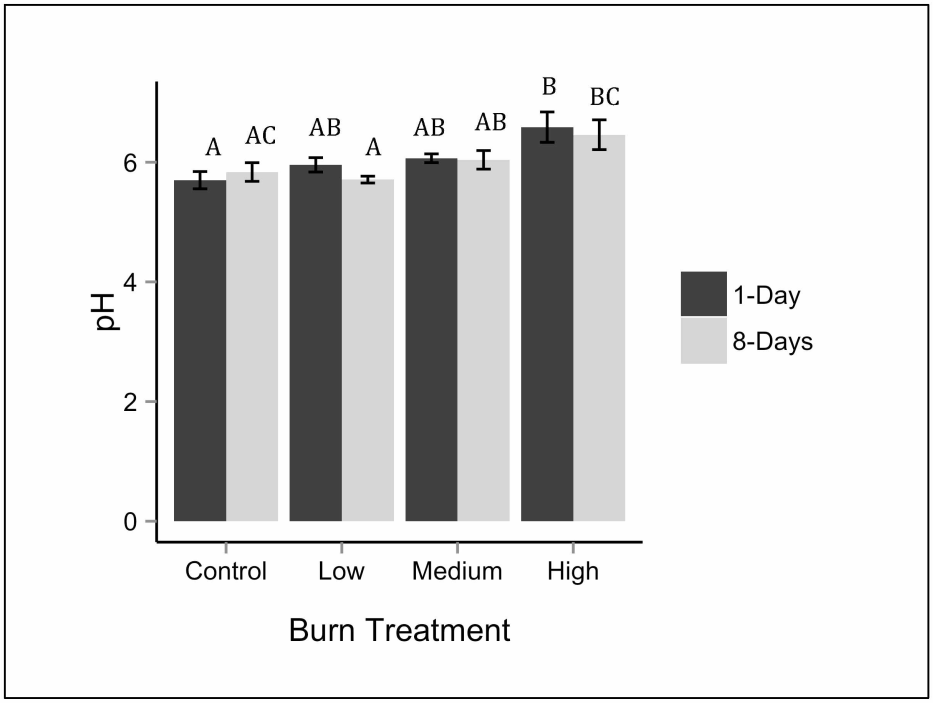


Figure 4: Soil pH
Mean organic layer pH, along a fire severity gradient created with experimental burns on July 6, 2012 in a mature Cajander larch forest near the Northeast Science Station in Cherskiy, Russia. Data are from 1-day and 8-days post-fire only. Error bars denote standard error; letters denote significance from a post-hoc Tukey's HSD test after fitting a mixed effects model.
There was no treatment effect on either soil moisture or pH in mineral layers.

Carbon Dynamics

Organic layer SOM (%) was positively correlated with remaining organic layer, and the 8-day and 1-year sampling points had significantly lower SOM than the 1-day sampling (fixed effects: slope; $p < 0.001$, 8-days; $p = 0.012$, 1-year; $p = 0.015$; Fig 5).

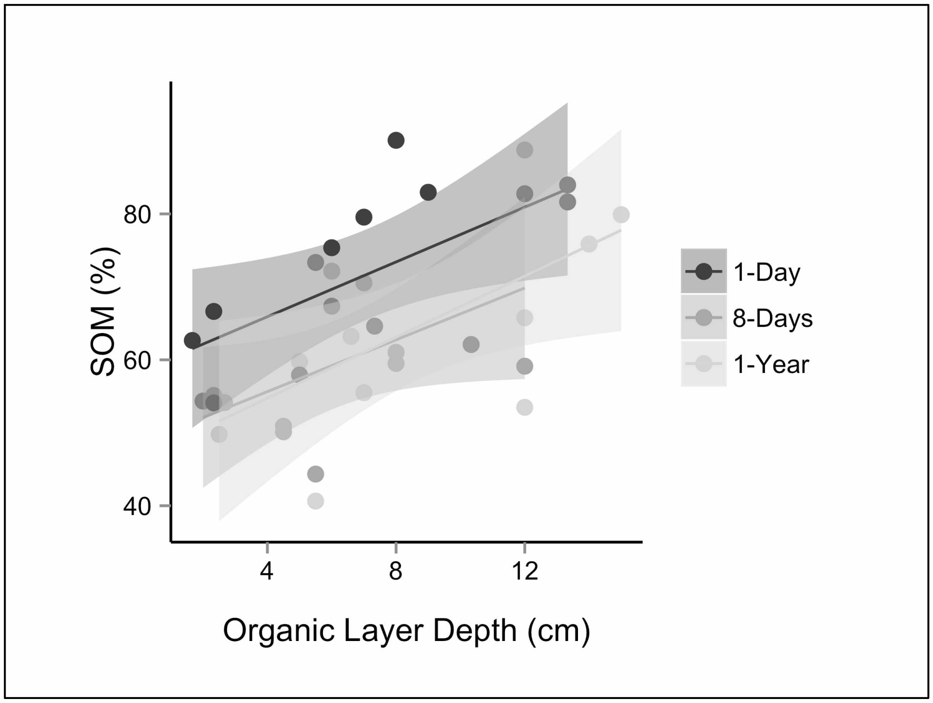


Figure 5: Soil Organic Matter
Organic layer % soil organic matter (SOM) as a function of residual organic layer depth, along a fire severity gradient created with experimental burns on July 6, 2012 in a mature Cajander larch forest near the Northeast Science Station in Cherskiy, Russia. Regression lines and 95% confidence intervals are from a mixed effects model.

Water-extractable DOC concentrations in the organic horizon increased significantly with fire severity (fixed effects: low; $p = 0.18$, medium; $p = 0.03$, high; $p = 0.01$, 8-days; $p < 0.001$, 1-year; $p < 0.001$), with the high severity plots averaging 4000 g C/ g soil, approximately 4x the concentration of unburned control plots at the initial post-fire sampling (Fig 6).

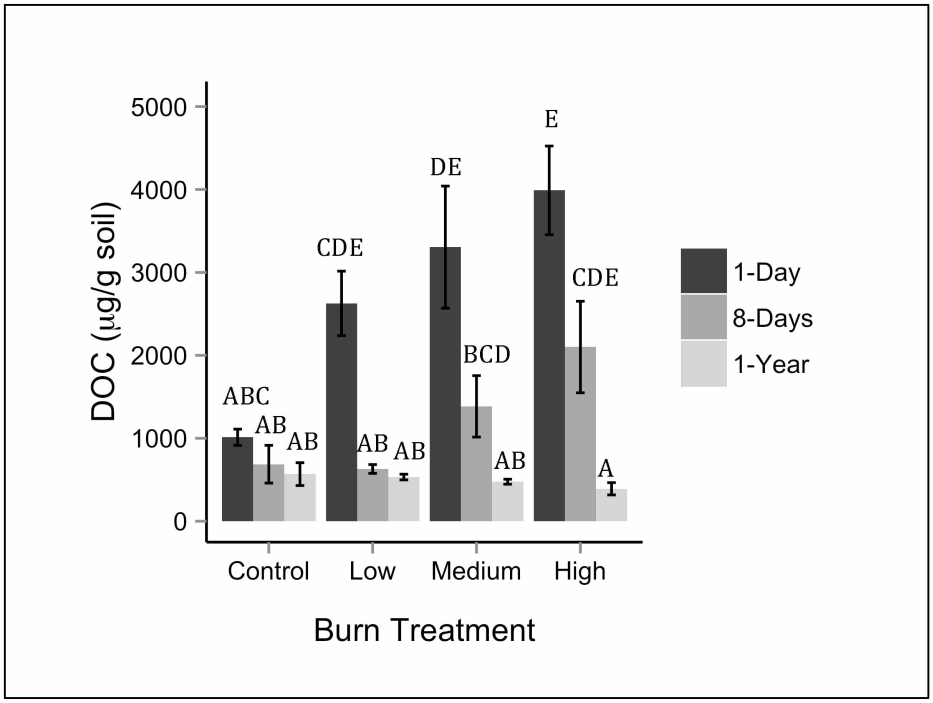


Figure 6: Dissolved Organic Carbon
Mean organic layer water-extractable dissolved organic carbon (DOC), along a fire severity gradient created with experimental burns on July 6, 2012 in a mature Cajander larch forest near the Northeast Science Station in Cherskiy, Russia. Error bars denote standard error; letters denote significance from a post-hoc Tukey's HSD test after fitting a mixed effects model.

This spike in DOC concentrations dropped by half by 8-day post-fire, but there was no significant treatment effect by 1-year post-fire. SUVA values from the water-extractable CDOM were significantly lower in the medium and high severity plots at the initial post-fire sampling (fixed effects: low; $p = 0.38$, medium; $p = 0.014$, high; $p = 0.012$, 8-days; $p < 0.01$, 1-year; $p < 0.001$), indicating lower aromaticity in these treatments (Fig 7).

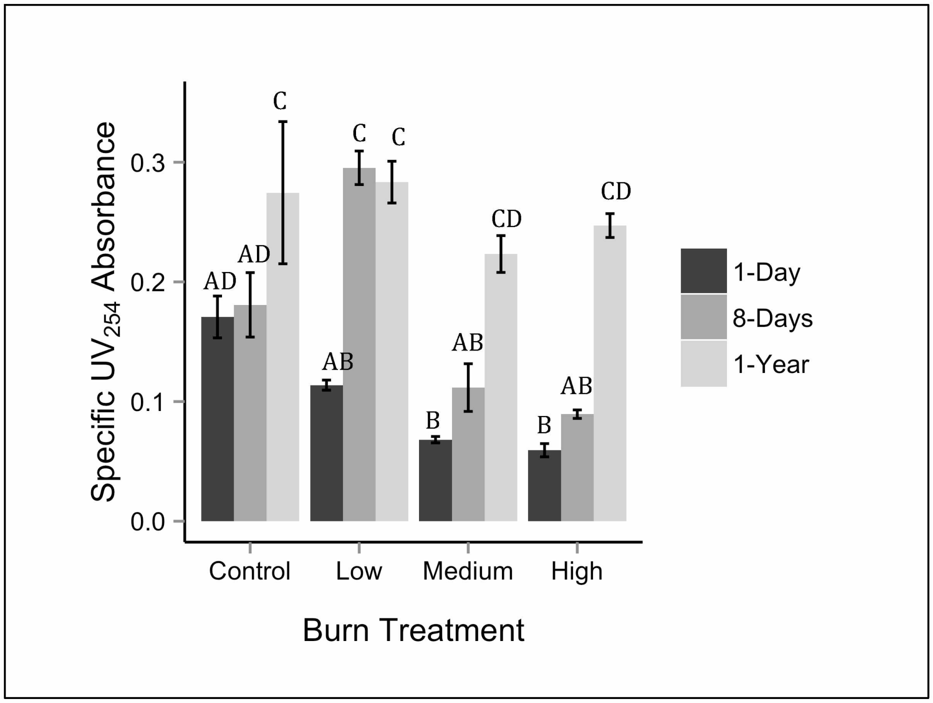


Figure 7: Dissolved Organic Matter Aromaticity
Mean organic layer dissolved organic matter aromaticity as indicated by specific UV absorbance, along a fire severity gradient created with experimental burns on July 6, 2012 in a mature Cajander larch forest near the Northeast Science Station in Cherskiy, Russia. Error bars denote standard error; letters denote significance from a post-hoc Tukey's HSD test after fitting a mixed effects model.

By 8-days post-fire, only the low severity plots were different from the control showing higher aromaticity, and by 1-year post-fire, all treatments were comparable to the control plots. The slope ratio (S_R) of water-extractable CDOM increased with fire severity (fixed effects: low; $p = 0.18$, medium; $p < 0.01$, high; $p < 0.01$, 8-days; $p = 0.12$, 1-year; $p = 0.04$), indicating lighter molecular weight compounds in the medium and high severity treatments (Fig 8).

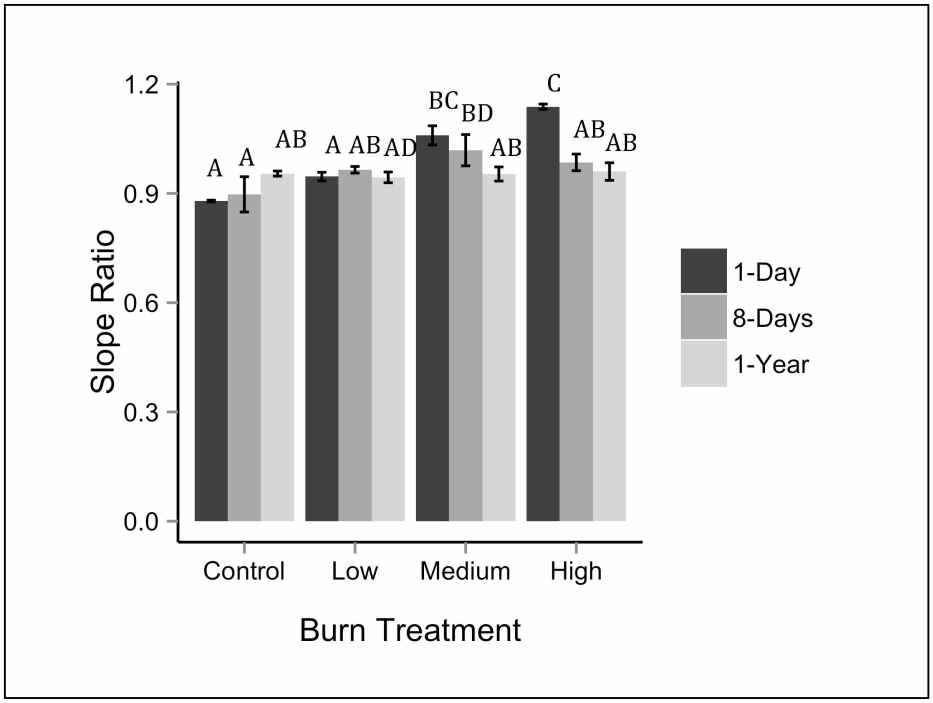


Figure 8: Dissolved Organic Matter Molecular Weight
Mean organic layer dissolved organic matter molecular weight as indicated by slope ratio, along a fire severity gradient created with experimental burns on July 6, 2012 in a mature Cajander larch forest near the Northeast Science Station in Cherskiy, Russia. Error bars denote standard error; letters denote significance from a post-hoc Tukey's HSD test after fitting a mixed effects model.

This effect was largely diminished by 8-days post-fire, and there was no significant treatment effect by 1-year post-fire. Neither the concentration nor the lability of C in the mineral horizons showed any effects from the fires.

Nutrient Dynamics

Water-extractable DON was very similar to that of DOC, with an initial increase in concentration with fire severity in the organic horizon that diminished greatly by 8-days post-fire and was gone completely by 1-year post-fire (fixed effects: low; $p = 0.22$, medium; $p = 0.03$, high; $p = 0.08$, 8-days; $p = 0.02$, 1-year; $p < 0.001$) (Fig 9), and no fire effect in the mineral horizons.

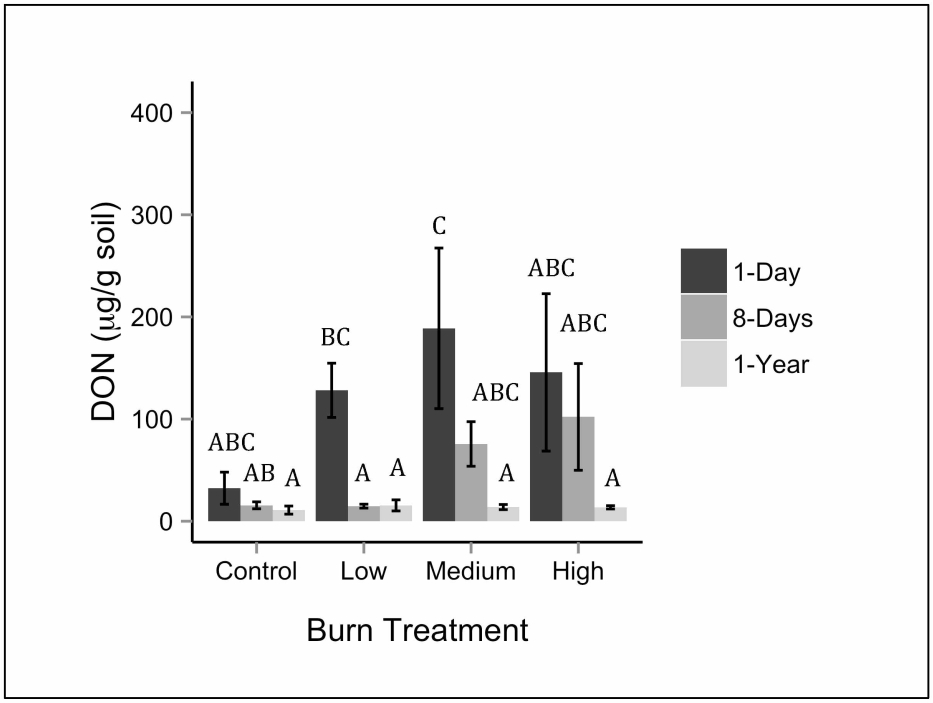


Figure 9: Dissolved Organic Nitrogen
Mean organic layer water-extractable dissolved organic nitrogen (DON), along a fire severity gradient created with experimental burns on July 6, 2012 in a mature Cajander larch forest near the Northeast Science Station in Cherskiy, Russia. Error bars denote standard error; letters denote significance from a post-hoc Tukey's HSD test after fitting a mixed effects model.

DIN concentrations from the organic horizon were greatly increased in the high severity treatments only and remained elevated by 8-days post-fire (fixed effects: low; $p = 0.19$, medium; $p = 0.57$, high; $p < 0.01$, 8-days; $p = 0.056$, 1-year; $p = 0.17$; Fig 10a).

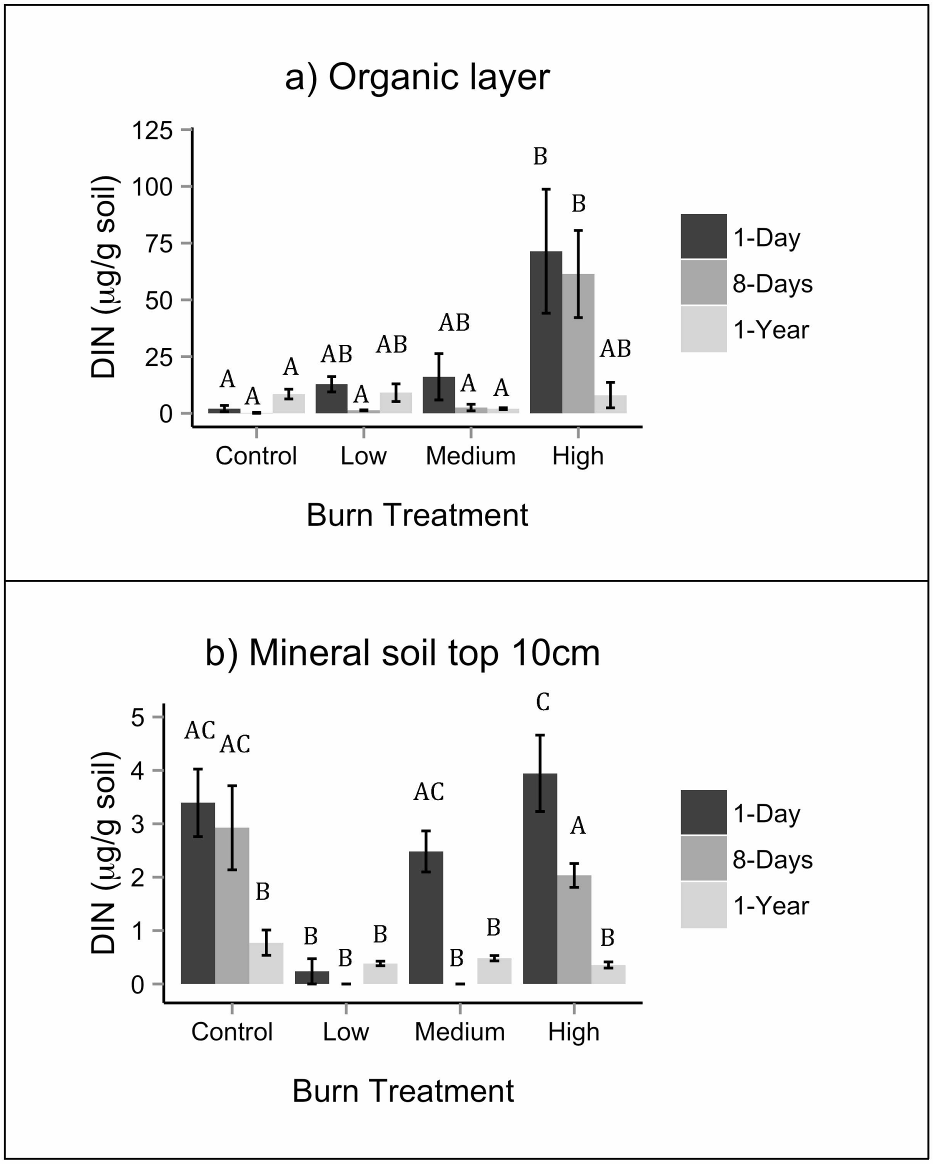
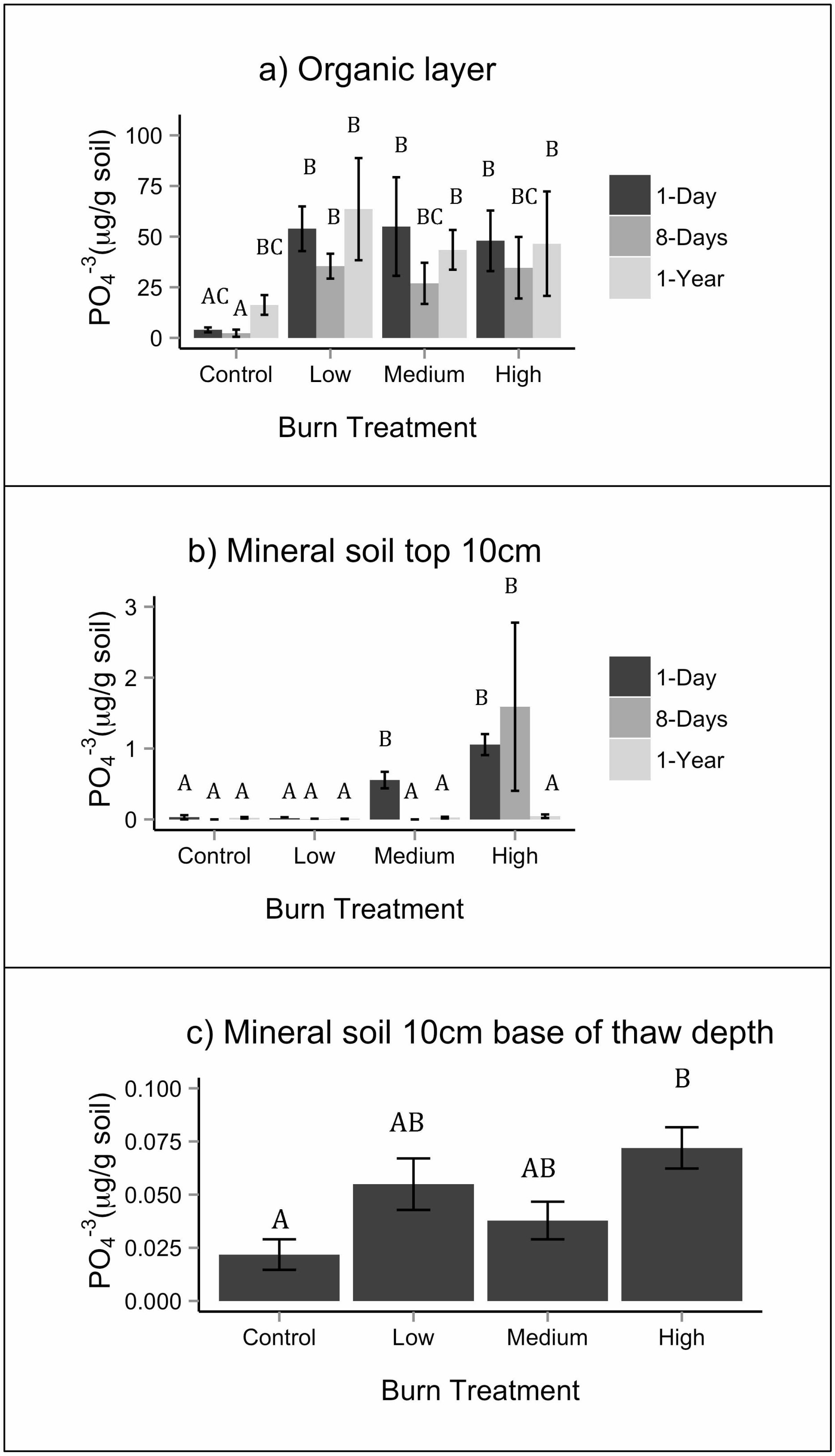


Figure 10: Dissolved Inorganic Nitrogen
Mean water-extractable dissolved inorganic nitrogen (DIN), along a fire severity gradient created with experimental burns on July 6, 2012 in a mature Cajander larch forest near the Northeast Science Station in Cherskiy, Russia. Error bars denote standard error; letters denote significance from a post-hoc Tukey's HSD test after fitting a mixed effects model.

By 1-year post-fire there was no longer a treatment effect. DIN concentrations in the top mineral horizon 1-day post-burn were significantly lower in the low treatments compared to both the control plots and other burn severities (fixed effects: low; $p < 0.001$, medium; $p = 0.02$, high; $p = 0.66$, 8-days; $p < 0.01$, 1-year; $p < 0.001$; Fig 10b). By 8-days post-fire, DIN concentrations in both the low and medium treatments were below levels of detection while the high severity treatments remained comparable to the control plots. By 1-year post-fire, all treatments were similar to the control plots.

Dissolved phosphate concentrations in the organic layer in all treatments were significantly and similarly greater than the control plots both initially and 8-days post-fire (fixed effects: low; $p < 0.001$, medium; $p < 0.01$, high; $p < 0.01$, 8-days; $p = 0.11$, 1-year; $p = 0.31$; Fig 11a).


a) Organic layer
PO_4^{-3}(µg/g soil)
100
75
50
25
0
AC
A
BC
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B
BC
B
Control
Low
Medium
High
Burn Treatment
1-Day
8-Days
1-Year
b) Mineral soil top 10cm
PO_4^{-3}(µg/g soil)
3
2
1
0
A
A
A
A
A
A
B
A
A
B
B
A
Control
Low
Medium
High
Burn Treatment
1-Day
8-Days
1-Year
c) Mineral soil 10cm base of thaw depth
PO_4^{-3}(µg/g soil)
0.100
0.075
0.050
0.025
0.000
A
AB
AB
B
Control
Low
Medium
High
Burn Treatment

Figure 11: Phosphate

Mean water-extractable phosphate, along a fire severity gradient created with experimental burns on July 6, 2012 in a mature Cajander larch forest near the Northeast Science Station in Cherskiy, Russia. Error bars denote standard error; letters denote significance from a post-hoc Tukey's HSD test after fitting a mixed effects model for a) and b) and an analysis of variance model for c).

By 1 year the phosphate concentrations remained high in the burned treatments, but the control plots increased, leading to no significant treatment effect. Dissolved phosphate from the top mineral layer also showed a strong treatment effect, where 1-day post-fire the medium and high severity plots were elevated (fixed effects: low; $p = 0.92$, medium; $p = 0.33$, high; $p < 0.01$, 8-days; $p = 0.35$, 1-year; $p = 0.02$). By 8-days post-fire only the high severity treatments were elevated, and by 1-year all were back to the level of the control plots (Fig 11b). The bottom mineral layer, however, exhibited increased dissolved phosphate in the high severity treatments compared to the control plots at the 1-year sampling point (ANOVA; $F_{3,8}=5.08$, $p=0.03$; Fig 11c).

Extracellular Enzyme Activities

Extracellular enzyme activities in the organic horizon responded linearly to fire severity. There was a significant increase in β-glucosidase activity with residual organic layer depth at all time points (fixed effects: slope; $p < 0.01$, 8-days; $p = 0.04$, 1-year; $p = 0.19$; Fig 12).

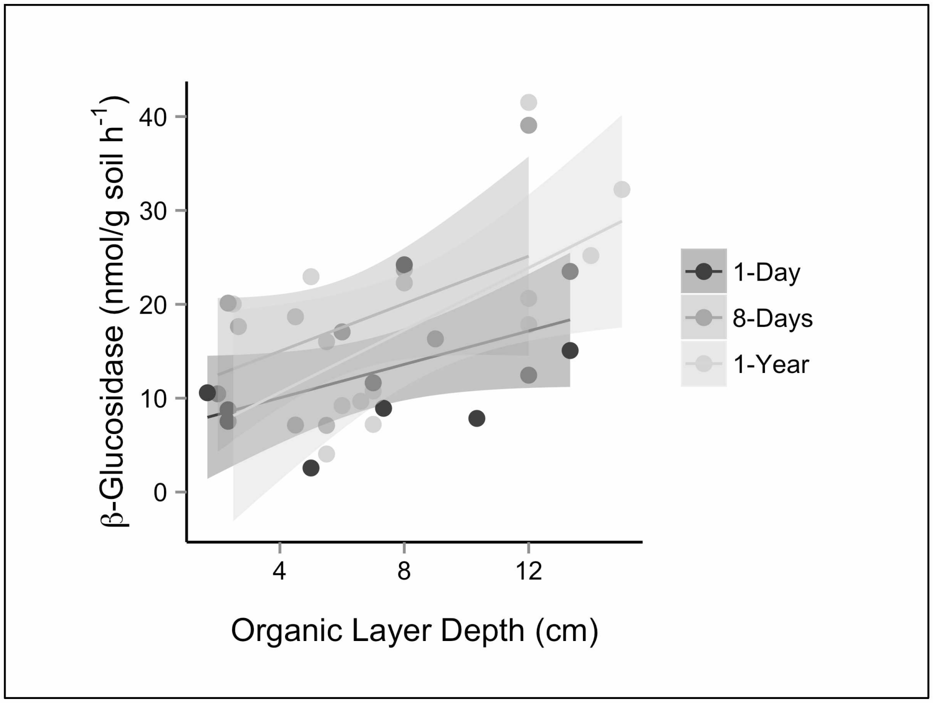

Figure 12: β-glucosidase Activity
Organic layer β-glucosidase activity as a function of residual organic layer depth, along a fire severity gradient created with experimental burns on July 6, 2012 in a mature Cajander larch forest near the Northeast Science Station in Cherskiy, Russia. Regression lines and 95% confidence intervals are from a mixed effects model.

There was also a significant relationship between β-glucosidase activity and soil moisture (slope = 0.45, $p < 0.01$), and the residuals of this regression no longer have a significant relationship to residual organic layer depth ($p = 0.14$). Phosphatase activity increased linearly with residual organic layer depth at all time points as well (fixed effects: slope; $p < 0.01$, 8-days; $p = 0.09$, 1-year; $p = 0.019$; Fig 13).

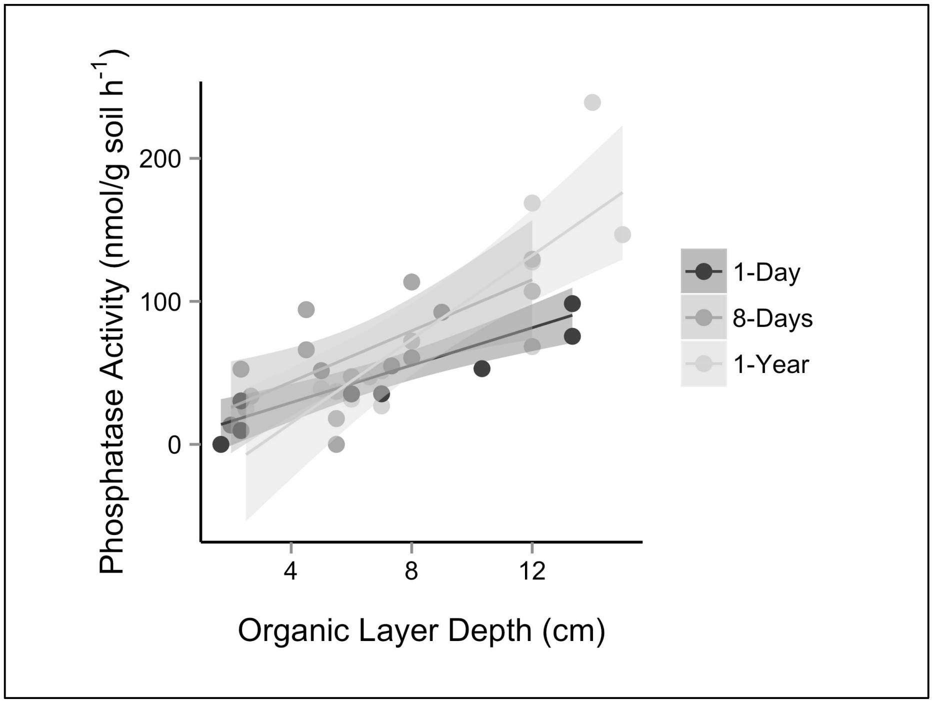

Figure 13: Phosphatase Activity
Organic layer phosphatase activity as a function of residual organic layer depth, along a fire severity gradient created with experimental burns on July 6, 2012 in a mature Cajander larch forest near the Northeast Science Station in Cherskiy, Russia. Regression lines and 95% confidence intervals are from a mixed effects model.

Soil moisture also has a positive correlation with phosphatase activity (slope = 2.05, $p = 0.027$). However, soil moisture alone could not explain phosphatase activity, as the model residuals still had a significant relationship to residual organic layer depth and time (fixed effects: slope; $p < 0.001$, 8-days; $p = 0.015$, 1-year; $p < 0.01$). Leucine aminopeptidase activity was negatively correlated with residual organic layer depth at the 1-day post-fire sampling (slope = -2.68; $p = 0.02$), showed no effect from fire at the 8-day sampling (slope = -1.58; $p = 0.54$), and positively correlated with residual organic layer depth at the 1-year post-fire sampling (slope = 21.04; $p = 0.012$; Fig 14).

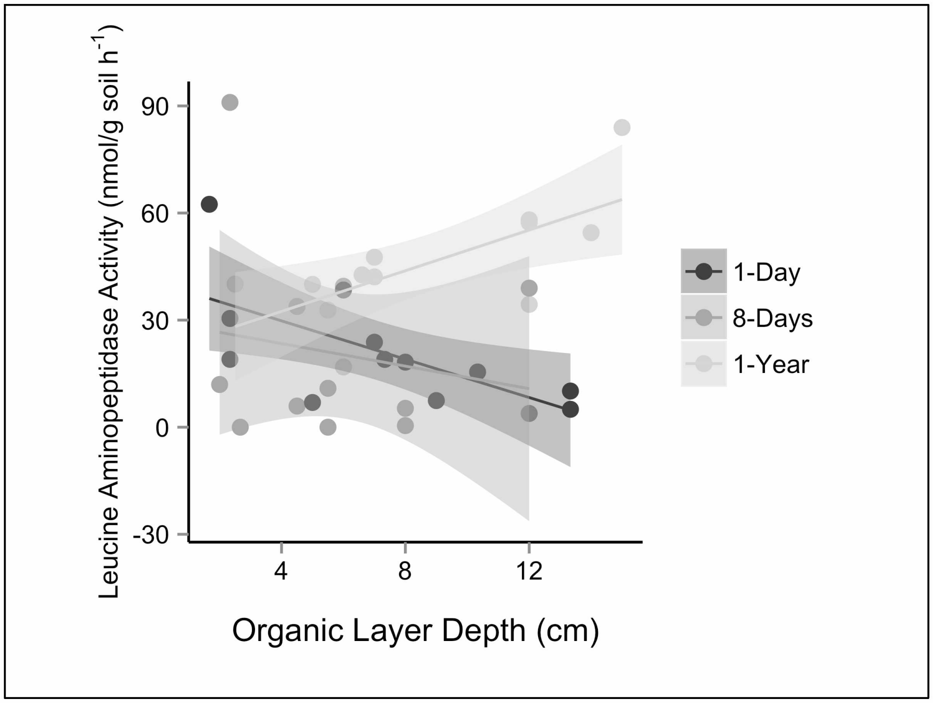

Figure 14: Leucine Aminopeptidase Activity
Organic layer leucine aminopeptidase activity as a function of residual organic layer depth, along a fire severity gradient created with experimental burns on July 6, 2012 in a mature Cajander larch forest near the Northeast Science Station in Cherskiy, Russia. Regression lines and 95% confidence intervals are from a mixed effects model.

Leucine aminopeptidase activity and soil moisture were not significantly correlated ($p = 0.42$). Fire severity had no effect on phenol oxidase activity, although there was an increase in activity between the first and second years of the study. The mineral horizon activities for all enzymes were very low with no treatment effects.

Soil Incubations

Samples from 1-year post-fire were incubated in the lab to measure respiration and net production rates of DOC, DON, and DIN. Fires significantly reduced soil respiration in the organic horizon in the medium and high severity treatments (ANOVA; $F_{3,8}$=5.83, p=0.021; Fig 15a).

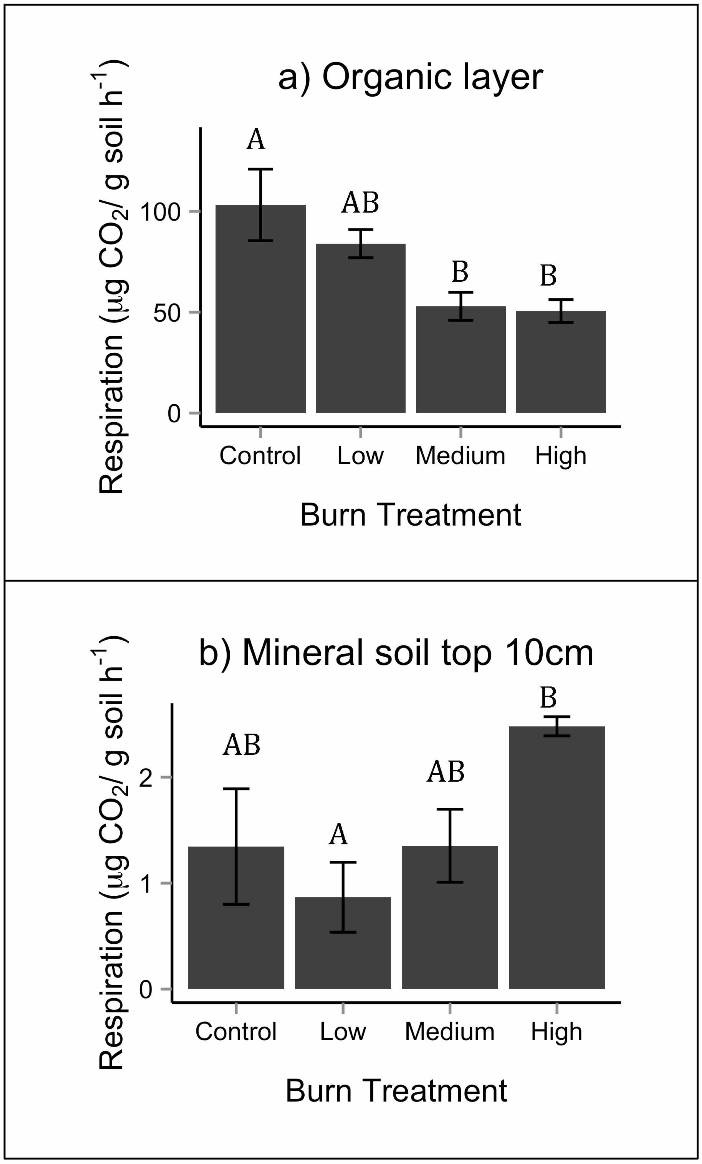

Figure 15: Soil Respiration
Mean soil respiration, 1-year post-fire, along a fire severity gradient created with experimental burns on July 6, 2012 in a mature Cajander larch forest near the Northeast Science Station in Cherskiy, Russia. Error bars denote standard error; letters denote significance from a post-hoc Tukey's HSD test after fitting an analysis of variance model.

The top mineral horizon showed a marginal effect with the high severity treatment having significantly higher respiration than the low treatment (ANOVA; $F_{3,8}$=3.53, p=0.068; Fig 15b). Soil respiration in both the organic and mineral horizons was positively correlated to soil moisture (organic; $r^2 = 0.64$, $p < 0.01$, mineral; $r^2 = 0.73$, $p < 0.001$). After accounting for soil moisture, there was no longer a relationship between soil respiration and treatment for either soil horizon. All fire treatments from the organic layer had net production rates for DOC, DON, and DIN near zero (ANOVA; $F_{3,8}$=9.9, p<0.01; $F_{3,8}$=10.8, p<0.01; $F_{3,8}$=7.38, p=0.01, respectively), while the control plots had a significantly negative net production rates (Fig 16).

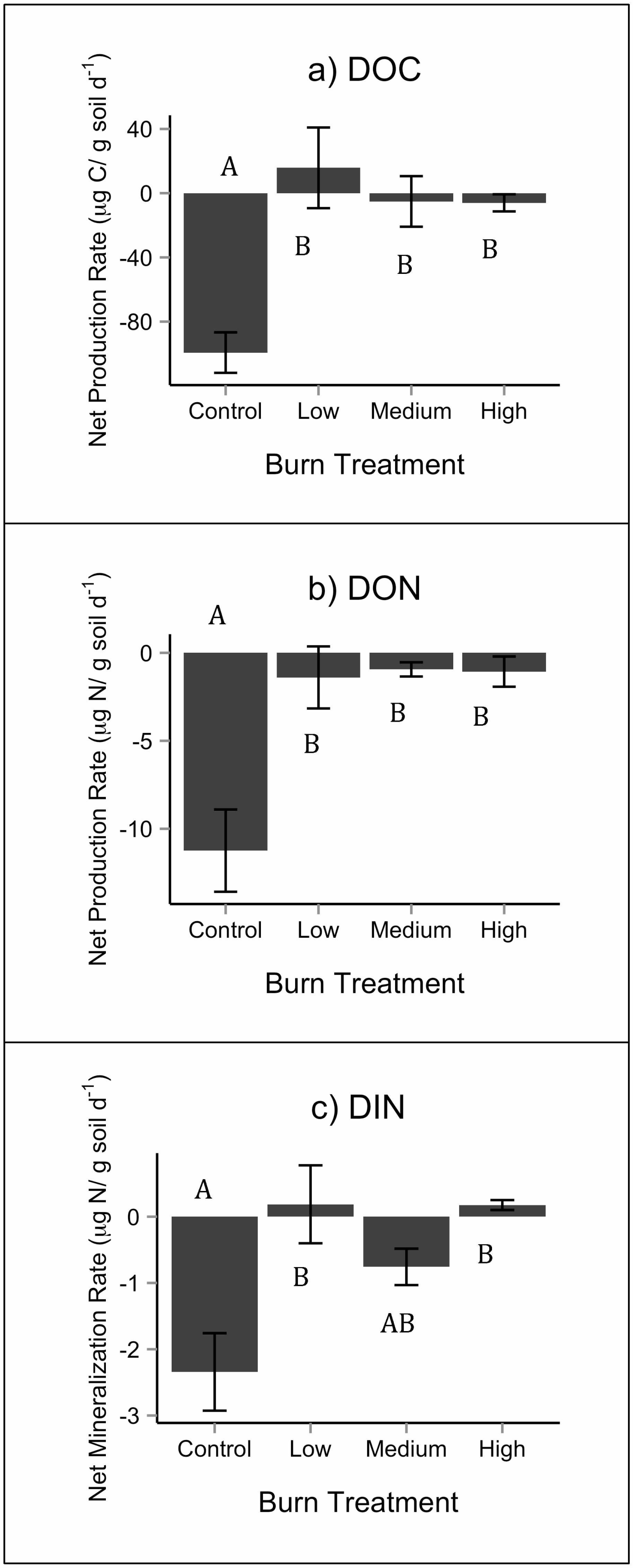
a) DOC
Net Production Rate (µg C/ g soil d-1)
40
0
-40
-80
A
B
B
B
Control
Low
Medium
High
Burn Treatment
b) DON
Net Production Rate (µg N/ g soil d-1)
0
-5
-10
A
B
B
B
Control
Low
Medium
High
Burn Treatment
c) DIN
Net Mineralization Rate (µg N/ g soil d-1)
0
-1
-2
-3
A
B
AB
B
Control
Low
Medium
High
Burn Treatment

Figure 16: Net Production Rates
Mean organic layer net production rates, 1-year post-fire, along a fire severity gradient created with experimental burns on July 6, 2012 in a mature Cajander larch forest near the Northeast Science Station in Cherskiy, Russia. Panel a) is dissolved organic carbon (DOC), b) is dissolved organic nitrogen (DON), and c) is dissolved inorganic nitrogen (DIN). Error bars denote standard error; letters denote significance from a post-hoc Tukey's HSD test after fitting an analysis of variance model.

Fire treatments had no effect on production rates within the mineral horizons. Soil moisture was negatively correlated with net production rates for DOC and DON but not DIN ($r^2 = 0.30$, $p = 0.04$; $r^2 = 0.27$, $p = 0.027$; $r^2 = 0.04$, $p = 0.25$; respectively). After removing the effect of soil moisture on DOC and DON net production rates, there was no longer a treatment effect.

Natural Fire Scars

We examined dissolved C, N, and P and measured extracellular enzyme activities from the organic horizon in two early successional larch stands that burned 7 and 11 years prior to sampling. Each stand was paired with an adjacent unburned stand. To compare the effects of fire in these stands, we calculated response ratios as the concentration or activity in the burned stand divided by that of the unburned stand. The response ratios of DOC and DON for the 11-year old fire scar were significantly less than one (t-test; t_4=-7.22, p=0.019; t_4=-4.76, p=0.04, respectively; Fig 17), and ratios for the 7-year old fire were different from one for DOC but not DON (t-test; t_4=-7.95, p=0.015; t_4=-2.06, p=0.18, respectively; Fig 17).

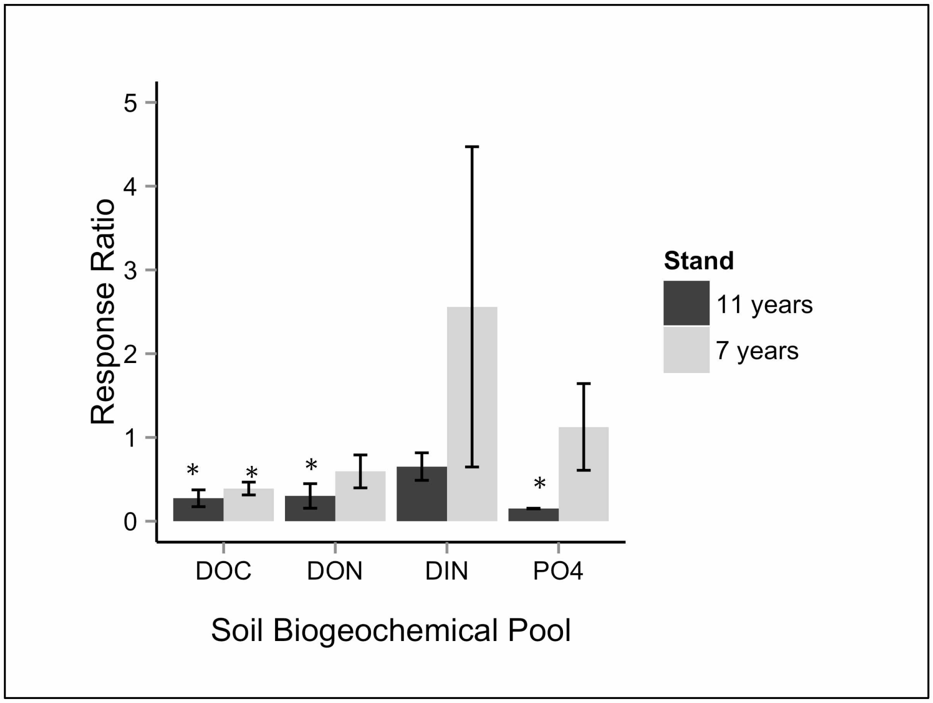

Figure 17: Fire Scar Response Ratios
Mean response ratio (burned:control) of water extractable dissolved organic matter and nutrients from the organic horizon of 7-year old and 11-year Cajander larch stands, sampled July 2013 near the Northeast Science Station in Cherskiy, Russia. Error bars denote standard error; star indicates t-test results significantly different from 1.

The response ratios for DIN were equivalent to one for both fires (11-year t-test; $p = 0.17$, 7-year t-test; $p = 0.5$; Fig 17). The response ratio for phosphate was below one for 11-years but not for 7-years ($p < 0.001$, $p = 0.83$, respectively; Fig 17). For both fire scars, phosphatase activity was significantly lower than the control stands (11-year; $t_4=-3.31$, $p=0.028$, 7-year; $t_4=-2.63$, $p=0.05$; Fig 18).

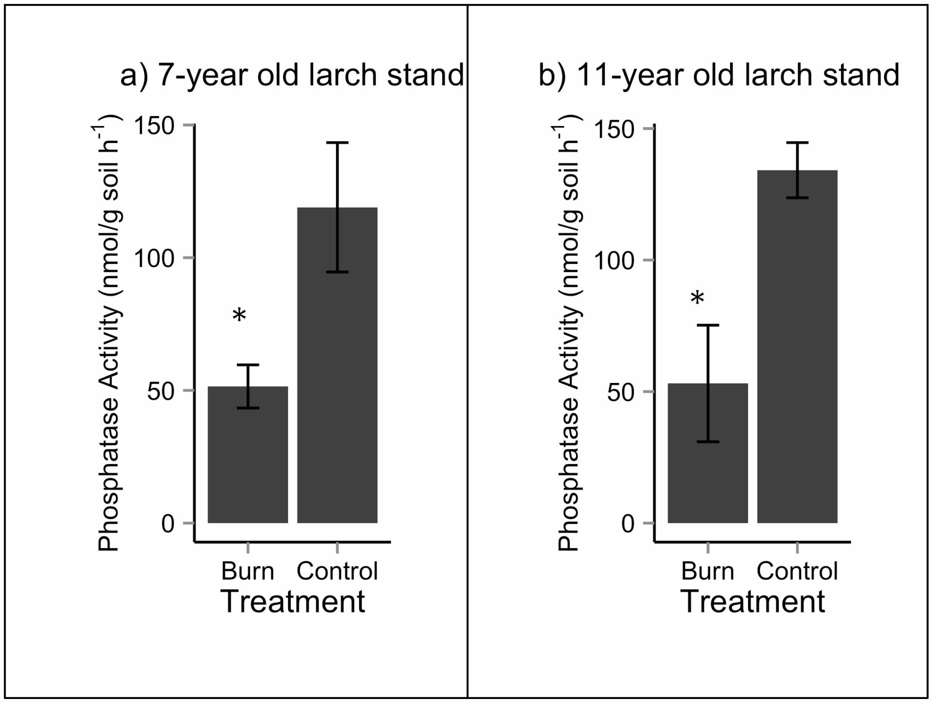

Figure 18: Fire Scar Phosphatase Activity
Mean phosphatase activity from the organic horizon of a) 7-year old and b) 11-year old Cajander larch stands, sampled July 2013 near the Northeast Science Station in Cherskiy, Russia. Error bars denote standard error; star indicates t-test results significantly different means.

The only other significant response to fire was lower β-glucosidase activity in the burned areas of the 7-year old fire scar (t-test; t_4=-4.42, p=0.011; Fig 19).

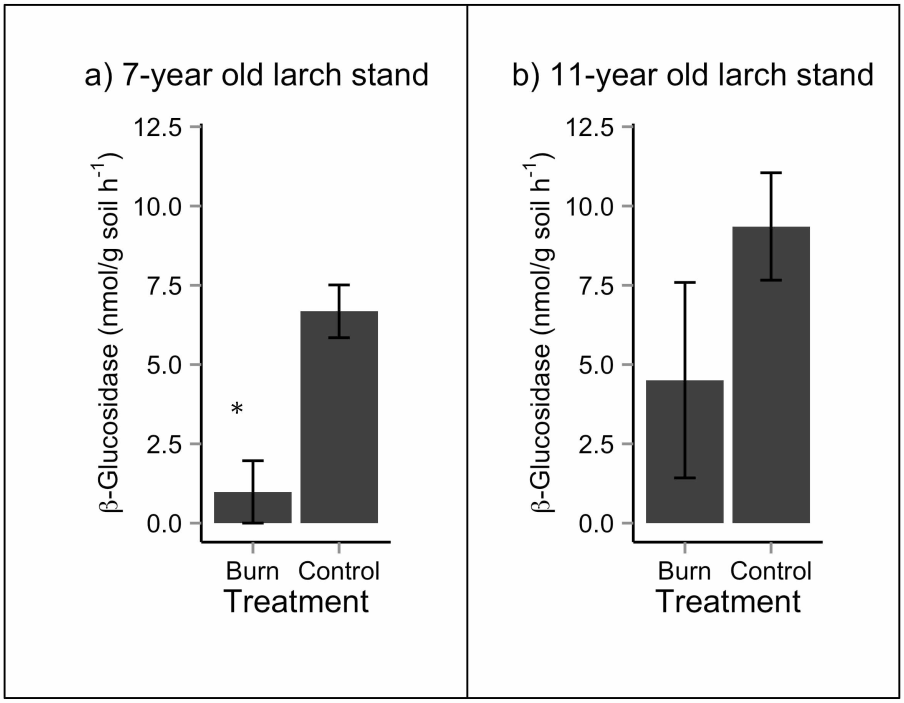

Figure 19: Fire Scar β-glucosidase activity
Mean β-glucosidase activity from the organic horizon of a) 7-year old and b) 11-year old Cajander larch stands, sampled July 2013 near the Northeast Science Station in Cherskiy, Russia. Error bars denote standard error; star indicates t-test results significantly different means.

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Discussion

Our findings support the hypothesis that combustion of the organic layer can result in a brief flush of resources. This initial increase in nutrients following fire has been described in other ecosystems, and it is sometimes, but not always, associated with a concurrent increase in microbial activity (DeLuca and Zouhar 2000, Choromanska and DeLuca 2001, 2002, Bárcenas-Moreno et al. 2011). Here, we observed mixed reactions in microbial activities. The reduction of β-glucosidase and phosphatase with increasing fire severity, which we observed at all time points, could be the result of lower active microbial biomass due to fire-induced mortality. However, this explanation does not account for the observed increase in leucine aminopeptidase activity with increasing fire severity. Therefore, these rate changes are most likely a response to substrate availability. Increased phosphate availability, which we observed following experimental burns, can suppress phosphatase activity (Sinsabaugh and Shah 2012). There are many more N-acquiring than P-acquiring enzymes, and they often liberate C as well as N (Allison and Vitousek 2005), which may have down-regulated B-glucosidase. The positive relationships between leucine aminopeptidase activity, DIN (in high severity treatments only), and DON we attribute to increased organic N, possibly derived from thermal mineralization of organic matter, inducing the production of enzymes to break it down.

The response of C cycling extracellular enzymes to an increase in labile C is less straightforward due to the variety of C compounds and associated enzymes. More than one enzyme might be required to fully break down a molecule; for example, a diverse set of enzymes must interact to break down polysaccharides due to the range of monomers, linkages, and chrystallinity (Sinsabaugh 2010, Sinsabaugh and Follstad Shah 2010, Moorhead et al. 2013). We observed a post-fire increase in soluble, less aromatic, and smaller molecular weight DOM. If these compounds are easily assimilated and soil microbes follow a simple induction-suppression response, this may explain the reduction in β-glucosidase activity. It also follows that β-glucosidase activity might have declined because microbes are diverting resources towards producing other, unmeasured, C cycling enzymes.

We found no treatment effect from fire on phenol oxidase activity at any time point in our study. Phenol oxidase activity has been found to both increase and decrease following fires in other studies (Hamman et al. 2008, Boerner et al. 2008, Allison et al. 2010). Decreased activity is often associated with a decline in fungi, which can produce large quantities of phenol oxidase, but are highly sensitive to fire and with long post-fire recovery rates (Treseder et al. 2004, Waldrop and Harden 2008, Bárcenas-Moreno et al. 2011). Conversely, soil microbes might increase phenol oxidase production following fires as a means to break down highly aromatic black carbon. These offsetting effects may explain the lack of response in phenol oxidase that we measured across treatments.

Studies of immediate changes in C pools following fires in other soil types describe greater losses of labile than recalcitrant fractions, that are not recovered a year later (Jiménez Esquilín et al. 2008, Martín et al. 2009, Wang et al. 2012). We observed increases in lability following fire that quickly returned to control levels. We only examined the water extractable DOM pool, however, and given that much of the C left behind from fire can be highly aromatic and water repellent, it is likely that the fraction of recalcitrant C pools also increased. In addition to being recalcitrant, black carbon has a high sorption capacity and can adsorb inorganic and organic compounds (Hart et al. 2005). The increase in DOM and DIN we noted 1-day post-fire was greatly reduced after only a week's time. This loss could be due to sorption, uptake, or infiltration and leaching (Hart et al. 2005). While we cannot distinguish between the potential mechanisms responsible for the rapid disappearance of the initial rise of DIN and DOM, we did measure an increase in phosphate in the mineral horizons. The phosphate increase in deeper horizons is likely due to leaching and infiltration from ash and organic horizons. Since DOM and DIN did not increase post-fire within mineral horizons, this could indicate preferential uptake of DOM and DIN over phosphate, prior to infiltrating into deeper soils. Alternatively, evidence of elevated phosphate could remain because phosphate easily adsorbs to mineral soils and so leaches at slower rates than DIN or DOM.

We hypothesized that in the long-term, more severe fires will decrease soil C, N, and P resources. Our results from C and N pools support this hypothesis, but not for P. The increases in DOC, labile C, and both organic and inorganic N were completely gone by 1-year post-fire. Phosphate remained elevated in the organic horizon, either because of slow assimilation or low leaching. In the mineral horizon, phosphate returned to unburned control concentrations in the top 10-cm. On high severity plots, phosphate remained elevated at the base of thawed mineral soils, likely due to leaching from shallower horizons, as heat transfer to this depth is highly unlikely.

Our results support our hypothesis that in the long-term, more severe fires will decrease microbial activities. Phosphatase activity remained suppressed 1-year post-fire in the burned plots, in concordance with the continued presence of elevated phosphate. Both β-glucosidase and leucine aminopeptidase activity also remained suppressed where there was less residual organic layer 1-year post-fire, despite labile C and N resources returning to levels equivalent to unburned controls. In addition to decreases in extracellular enzyme activities, soil respiration declined in burned plots relative to unburned plots, but DIN and DOM net production rates increased. Given that all other activities were lower on burned plots, the net increase in production rates was likely due to reduced immobilization rates as opposed to an increase in gross production rates. This could be explained by a smaller active microbial biomass often observed for years after fires, especially in boreal forests (Dooley and Treseder 2011). Lower active microbial biomass after fires has been attributed to the loss of SOM (Hart et al. 2005), which our results support: SOM declined with burn severity and had not recovered by 1-year post-fire. The year after the plots burned, soil moisture was lower for all treatments and control plots, and also declined with increasing fire severity. If soil microbes were drought stressed, this could contribute to a smaller active microbial biomass. This conclusion is supported by the fact that soil respiration, β-glucosidase activity, and DOC and DON net production rates could be fully explained by soil moisture.

We sampled soils within two early-successional larch stands (7 and 11 year post-fire) near our experimental burns, with the goal of placing our results from the experimental burns in the context of natural wildfires after a longer recovery time. Organic soils within both natural burns had lower water-soluble DOM than their unburned counterparts, which is likely a consequence of reduced SOM. Thus, we might expect DOM in our experimental burns to continue declining. Phosphate was lower in the 11-year old stand than in its paired unburned stand, but comparable between the 7-year old stand and its paired control stand. The control stands for the 11-year old fire scar had about double the phosphate of the control stands for the 7-year old fire scar. The discrepancy between response ratios of phosphate concentrations could be due to the 4-year difference in recovery time, or differences in fire severity, for which we have no measurements. Despite having lower phosphate concentrations, phosphatase activity was lower in both naturally burned sites than in their control stands, possibly a consequence of a less active microbial biomass. This interpretation is supported by lower β-glucosidase activity in burned stands, although only significantly so in the 7-year old stand.

The way in which fire severity affected soil biogeochemical pools and microbial activities depended on both the element and process. The initial increases in C, N, and P were nonlinear responses: rather than relating linearly to residual organic layer depth (i.e., fire severity), differences were only significant at certain thresholds of burn severity. The high severity burns stood apart for C and N pools, with far greater increases above the control plots than lower severities, whereas for P all levels of burn severity were equivalently elevated above the control plots. Enzyme activities responded linearly to the loss in organic matter from fires, along with edaphic variables like soil moisture and SOM content. Soil respiration was only different from control plots in burns of at least medium severity, and net production rates of DON, DIN, and DOC, also showed a non-linear response where any degree of fire severity had the same effect. This varied combination of threshold and linear response curves to fire severity could help explain why there is such a range in effects of fire on soil microbial dynamics (Hart et al. 2005, Boerner et al. 2008, 2009, Dooley and Treseder 2011, Ginzburg and Steinberger 2012, Wang et al. 2012, Holden and Treseder 2013).

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Conclusions

We have demonstrated that fires in organic-rich permafrost ecosystems can create a substantial increase in nutrients and labile carbon immediately (1-8 days) after the most severe fires. The longevity of this fertilization varies by element, with PO_4^{3-} remaining in abundance for more than a year, but C and N declining within days. Terrestrial boreal ecosystems are most often limited by N, yet it is unlikely that recovering vegetation will have the opportunity to take advantage of this initial increase in N supply following fires given its transience. Over the long-term, an increase in net N mineralization rates could lead to increased nutrient availability for plants. However, a less active microbial biomass would also process SOM more slowly, and decreased rates of extracellular enzyme activities would result in less nutrients being liberated. The interaction of different nonlinear and linear response curves of biogeochemical pools and rates to fire severity has the potential to create a wide variety of circumstances for soil microbial communities following fire. Given that wildfire severity is often heterogeneous, more research is needed to determine why processes respond differently to fire severity, for example at what temperature or fuel loads certain mechanisms have stronger influences. Our results show significantly lower soil respiration in sites where at least half the organic layer was consumed by fire. This represents an important mechanism that could mitigate initial C losses from the fire in permafrost-dominated ecosystems. The changing fire regime in permafrost ecosystems has the potential to alter soil microbial community dynamics, the retention of nutrients, and the stoichiometry of C, N, and P availability.

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